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POPULATION DYNAMICS AND YIELD OF A MOOSE POPULATION WITHOUT PREDATORS

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ABSTRACT: Population dynamics, potential rate of increase (r_p), and potential yield of a moose population with no predators in south-central Sweden during 1980 through 1988 are described. Except for 2-year-old females (0.50 calf/female), age specific natal rates were high and stable between age classes ($\bar{x}=1.17$ calves/female for females ≥ 3 yrs). High natality rates in combination with low annual non-hunting death rates (calves=1%; adults=5.6%), and negligible dispersal rates (<1%) yielded a potential rate of increase (r_p) in the Grimsö moose population of 0.40. Consequently, 50% of the winter population could potentially be harvested each autumn if the population was maintained at the same density. With a winter density of 1.3 moose/km², a high annual yield was achieved in terms of meat (75 kg/km²) and number of killed animals (0.65 moose/km²). Under these circumstances hunting pressure must be high and male biased. The risk of dying (mainly through hunting) before 5 years of age was >90% among bulls and 70% among females. Selective harvesting on low-productive females in conjunction with high hunting pressure on bulls may further enhance the annual potential rate of increase to at least 60% of winter population. In other areas in southern Sweden the potential rate of increase may even exceed this rate by higher age specific natality.

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The moose population in Fennoscandia increased rapidly in the 1970's (Cederlund and Markgren 1987, Nygrén 1987, Østgård 1987). In Sweden the most dramatic changes occurred in the northern forest dominated regions where winter moose density increased fivefold within a decade (Cederlund and Markgren 1987). Although moose density has been reduced in recent years in Sweden total harvest approximated 140,000 in 1989 (Annual statistics from the Sportsmens' Association).

The increase in moose numbers was probably due to several factors such as favourable food conditions, regulated hunting, and low non-hunting mortality (Cederlund and Markgren 1987). The harvest system in Sweden is based on an area-quota system with primary objectives of minimizing damage to pine (*Pinus silvestris*) plantations and to reduce number of moose-vehicle accidents. The upper limit for moose carrying capacity is set by socio-economic interests and not by biological factors (Haagenrud *et al.* 1987). Hunting teams are directed to follow manage-

ment programs, which involve selective hunting of different categories of moose. In this way, kill quotas with 30 to 60 % calves are commonly achieved. Population density is estimated alternatively from aerial surveys (Tärnhuvud 1988), a system based on hunters' observations (Karlsson *et al.* 1988), or just by local managers' guesses. Although there have been differences in local hunting policies, the major goal has been to maintain a sustainable yields in terms of a high moose harvests.

High fecundity rates have been documented in several regions in Sweden (Markgren 1969, Stålfelt 1974) and calf recruitment $\leq 70\%$ of the previous winter populations is common (Stålfelt 1977). Average potential rate of increase approximates 50% of winter population, which appear equal to annual harvests. Most harvest programs have been relatively primitive in that they do not consider density dependent variations or weather related effects on moose demographic parameters. Hunting efficiency is high (70-90% of permitted kill quotas) and the organization in specific hunting teams adminis-

tered by local hunting authorities may allow efficient sampling of demographic data.

Our objectives were to estimate mortality, natality, emigration and immigration of a high density (1.3-2.3 moose/km² after hunt) moose population with adequate food resources, mild winters, and no mortality due to predators. We also wanted to calculate the potential rate of increase (r_p ; Caughley 1977a) and model how different sex and age distributions may affect yield in terms of number of moose in the kill and meat (kg/km²).

STUDY AREA

The study was conducted at the 140-km² Grimsö Research Area located in southcentral Sweden (59° 5' N, 15° 5' E). Most of the area is a rugged plateau with elevations of 100-150 m. Topography is low with flat ridges with till and boulders interspersed with bogs and swamps. The area consists of 72% forests, 20% bogs and swamps, and 8% uplands.

Mature forest stands are dominated by Scots pine (*Pinus silvestris*), Norway spruce (*Picea abies*), birch (*Betula* spp.), aspen (*Populus tremula*), and willows (*Salix* spp.). Most mature stands are harvested by clear cutting and replaced by planting. Rotation is approximately 90-100 years. Early successional stages after logging consist of birch, aspen, willow, and other deciduous species, with an understory of wavy hair grass (*Deschampsia flexuosa*), bilberry (*Vaccinium myrtillus*), lowbush cranberry (*Vaccinium vitis-idaea*), and heather (*Calluna vulgaris*).

Logging has fragmented the forest into subunits of varying successional stages. Approximately 70% of the stands are 3-10 ha.

Temperatures vary from 35 to -30°C; the mean daily temperature is 16.3 and -4.4°C in July and January, respectively. The ground is normally snow covered from late December to late March. Mean snow depth on 15 February is 27 cm. Annual precipitation averages 669 mm (Swedish Meteorol. Hydro. Inst. 1970-80).

MATERIAL AND METHODS

Harvest. Annual harvest quotas in Grimsö and adjacent areas were set by local hunting authorities and based on aerial surveys (see below). After a reduction of the population (high kill quotas) in the early 1980's the goal was to maintain a stationary population density of approximately 1.0 moose/km² after hunt (winter) each year. Hunting quota was set to 0.5 moose/km² annually (county's central hunting board).

During the harvest (October-December) in 1980-1988 data on sex, age, and weight, were obtained from 417 calves and 458 adults (≥ 1.5 yrs). Lower jaws from all animals, carcass weight (kg), date and place of kill were provided by hunters according to a standard procedure.

Aging was done by tooth wear to identify calves and yearlings (1.5-yrs-old) (Skuncke 1949), and by counting annuli in the cementum of the 1st molar (M1) (Mitchell 1967, Markgren 1969). Weight was equal to carcass weight (bled without viscera, skull, hide and lower legs) and measured to nearest kg. Late May was assumed to be the peak of the birth (Markgren 1969). Therefore, calves born the previous year were classified as yearlings during June (1-yr-old); animals between 24-36 months as 2-yr-olds, and so on.

Aerial surveys. Aerial surveys were done by helicopters (by Hughes 300, Hughes 500 or Ecorille AS 350) during January-March each year from 1981-1988. Total counts of moose, including age and sex were determined on the entire Grimsö Research Area from transects. Mean search area per hour was approximately 1,500 ha. The surveys began within two days after the end of a snow fall, at mean snow depth >30 cm and when snow was normally still covering tree branches. Depending on weather conditions, time since snow fall, experience of the observation team, survey intensity, etc, each moose density estimate was corrected by a sightability correction factor (Tärnhuvud 1988). All moose were

aged as adults or calves and sexed by antlers and presence or absence of vulval patch (Mitchell 1970).

Non-hunting mortality. Non-hunting mortality was calculated by counting carcasses found within Grimsö Research Area. The entire study area was searched at least once a year through activities associated with different research projects, aerial and ground surveys, and hunting. All radio marked moose which died were found and reported ≤ 1 yr by other people than the moose researchers. We therefore believed that most non-hunting mortality was located. Total moose mortality was calculated as the sum of hunting, traffic accidents, and residual mortality (diseases, starvation, predation, age senility etc.).

Radio marking. Data from radio marked animals were used to estimate emigration and immigration (17 males and 31 females) and natality rates ($n=67$) (here defined as calves/ marked female in autumn). Home range fidelity among adult females and dispersal rates among subadults has previously been analysed

for the Grimsö moose population during 1983-1989 (Cederlund and Okarma 1988, N. G. Cederlund and H. K. G. Sand unpubl. data).

The Model. Using the demographic data presented in Table 1, we calculated the potential rate of increase (r_p) of the moose population at Grimsö over one year. In a simple model we also simulated alternative sex and age distributions that was supposed to prevail in other populations in Sweden (Sand and Cederlund unpubl. data). We assumed emigration and immigration did not occur in the Grimsö area.

The following parameters were used:

1. The number (N_0) and sex ratio in the initial population was equal to the winter population found during the aerial survey in 1988 (91 females, 43 males, and 45 calves). The winter population was equal to the population just prior to the following reproductive season.
2. Age distribution (Ar_f) as calculated from the calf cohort analyses (Table 1).

Table 1. Life-table for the calf cohorts born in 1983 and 1984. The start population number ($n=241$) was calculated as the sum of all calves killed in autumn 1983 and 1984 and those found alive in the aerial survey during the following winter in 1984 and 1985. The cohorts were pooled to increase sample size and minimize the annual random variation in hunting mortality on specific age classes.

Age	MALES				FEMALES					
	lx	dx	qx	Am	lx	dx	qx	Af	Arf	mx
0	100	48	0.48		100	41	0.41			
1	52	26	0.50	44.4	59	17	0.28	30.3		
2	26	8	0.29	22.2	42	7	0.16	21.5	30.9	0.5
3	18	6	0.32	15.4	35	4	0.09	17.9	25.7	1.19
4	12	3	0.27	10.3	31	3	0.08	15.9	22.8	1.14
5+	9	9	1.0	7.7	28	28	1.0	14.4	20.6	1.19

Age - age in years.

lx - number of individuals alive at the start of each age class and standardized to start with 100.

dx - number of individuals dying in each age class, calculated as the sum of all mortality causes.

qx - mortality rate (dx/lx).

Am - age distribution (%) among adult (≥ 1 yr) males calculated from lx.

Af - age distribution (%) among adult (≥ 1 yr) females calculated from lx.

Arf - age distribution (%) among reproducing (≥ 2 yrs) females calculated from lx.

mx - natality rate calculated as the average number of calves/ marked female in autumn.

3. Natality rate (l_x) as observed from radio marked females (Table 1).

Calculation of the rates of increase:

$$1. \sum l_x m_x = R_0$$

Where: l_x is the number of females in each reproducing age class, m_x is the age specific natality rates and R_0 the number of calves in the following autumn.

$$2. N_0 + R_0 = N_t$$

Where N_0 is the total population number in winter 1988, and N_t the total population number in winter 1989 if hunting did not occur.

$$3. N_t / N_0 = \lambda \text{ and } \ln \lambda = r_p$$

Where λ = finite rate of increase and r_p is the potential rate of increase in the population.

Alternative data applied in the winter population 1988 (N_0) for modelling population growth:

1. Three sex ratios among adults (1:1, 1:2, and 1:3 males/female).
2. Two age distributions among reproducing females: Arf 1 = calculated from the life-table in the Grimsö population, Arf 2 = age distribution with more reproducing females in higher age classes, which occur in other moose populations (H. K. G. Sand and G. N. Cederlund unpubl. data) (Table 1).

RESULTS

Demography in the moose population at Grimsö

Population density. The moose population at Grimsö peaked in 1981 at an average density of 2.3 moose/km² (309 moose in total). Heavy hunting pressure during subsequent years reduced population density from 1.9 moose/km² in 1985 to 1.3 moose/km² in 1988.

Mortality. Annual hunting mortality averaged 40% of the previous winter population. Harvest of adult moose was skewed to males (\bar{x} =0.76 female/male). The average proportion of calves relative to adults in the harvest was 48% (ranging from 40% to 51%).

Traffic accidents were the second largest cause of mortality averaging, 6.0 adults/year (3.7% of winter population), and 0.5 calves/year (0.6% of winter population). We did not include postnatal mortality among calves during summer because we calculated rate of increase with calves/cow in autumn.

Residual mortality was calculated from carcasses found in the area and approximated 2.7 adults/year (<2% of the winter population), and 0.5 calves/year (0.6% of the calves in winter population).

Sex ratio. Adult sex ratio during winter (aerial counts) were biased in favour of females averaging 2.5 females/male, ranging from 3.3 in 1985 to 2.1 in 1981 and 1988. Skewed sex ratios were maintained by continuous selection for males in the harvest (see also Age distribution). Juvenile sex ratio in harvest was on average close to 50:50 but varied slightly between years. We assumed that calves were shot randomly with respect to sex.

Age distribution. We did not consider harvest data to fully reflect the standing age distribution in the population at Grimsö. Therefore, a cohort analysis was used in a life table to reconstruct age distribution of 2 cohorts ($n=241$ calves) born in 1983 and 1984 as they passed through the population. Mortality rates including harvest and non-hunting mortality were applied across ages. Adult age distribution was calculated for 5 age classes (1, 2, 3, 4, and 5+ yrs-old), and differed significantly between sexes ($\chi^2 = 13.4$, $df = 5$, $P < 0.01$) (Table 1). This discrepancy was probably caused by higher hunting pressure on males compared to females, resulting in a lower average age among males in the population. The risk of dying decreased with age, from being 0.45 among calves to less than 0.1 among females older than 4 yrs, while males in the latter age class had a death rate of almost 0.3. Consequently, the risk of dying before 5 yrs was > 90% for males compared to 70% for females.

Natality. Age specific natality rates were

achieved from the observed number of calves per marked female with known age in autumn. Natality rates were almost independent of age except for the youngest reproducing age class. Observations of 2-year-old females, showed only 50% to have a calf at heel in autumn while older females (3, 4 and 5+ yrs) showed little variation between age classes and had on average 1.17 calves/female (Table 1).

Movements. The previous studies on moose movements at Grimsö clearly showed that young individuals (≤ 4 yrs) were highly philopatric and had a high fidelity to previous years' and seasonal home ranges (Cederlund and Okarma 1988, G. N. Cederlund and H. K. G. Sand unpubl. data). No moose abandoned their natal area completely (overlap of following yearly home range areas $>5\%$). Although seasonal movements occurred, distances between local sites were small in relation to average, annual home range (female $\bar{X}=13 \text{ km}^2$ irrespective of age, while male home range was correlated to age, $>30 \text{ km}^2$ for males ≥ 4 yrs old). We therefore considered the

moose population at Grimsö to be sedentary with little or no emigration. No data were available on immigration. Since moose density only changed slightly during the study and topography and food resources were the same outside the research area, we considered immigration to be insignificant.

Rate of increase (r_p) and yield. The potential rate of increase (r_p) varied from 0.33 ($\lambda = 1.39$) to 0.44 ($\lambda = 1.55$) depending on the adult sex ratio and age distribution (Fig. 1 and 2). As a result of the low variation in natality rate between age classes, sex ratio was more important explaining differences in the rate of increase than was age distributions.

Based upon 1988 spring population we assumed that 88 animals were recruited into the autumn population. The pre-harvest population density then approximated 2 moose/ km^2 . Assuming that calves and adults each constitute 50% of the total harvest and that carcass weights averaged 70 kg and 160 kg for calves and adults, respectively (N. G. Cederlund and H. K. G. Sand unpubl. data), the population produced a meat yield of 75.0

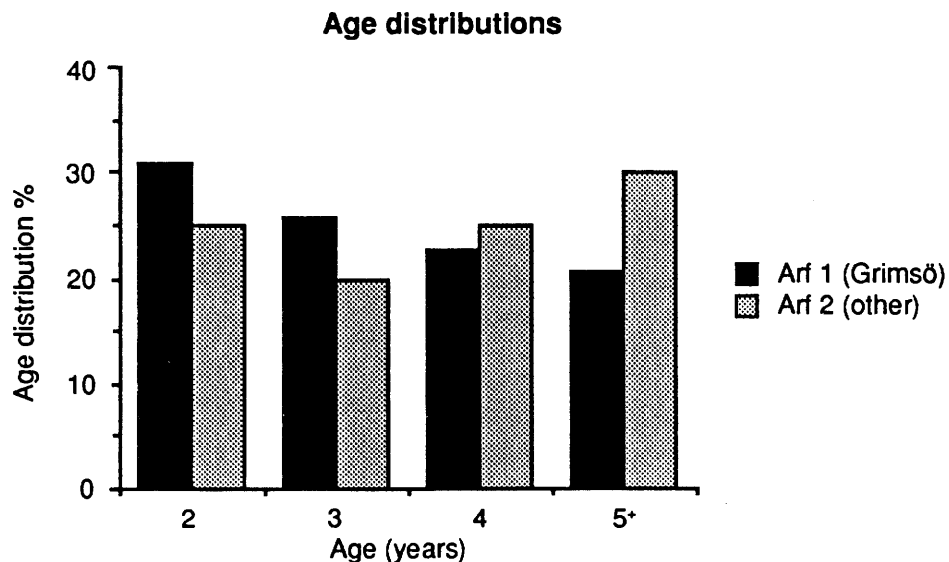


Fig. 1. Age distributions among reproducing females (≥ 2 yrs) in the Grimsö population calculated from the life-table analyses (Arf 1) (Table 1), and age distribution with a higher proportion of old females presumed to occur in other moose populations in Sweden (Arf 2) (G. N. Cederlund and H. K. G. Sand unpubl. data).

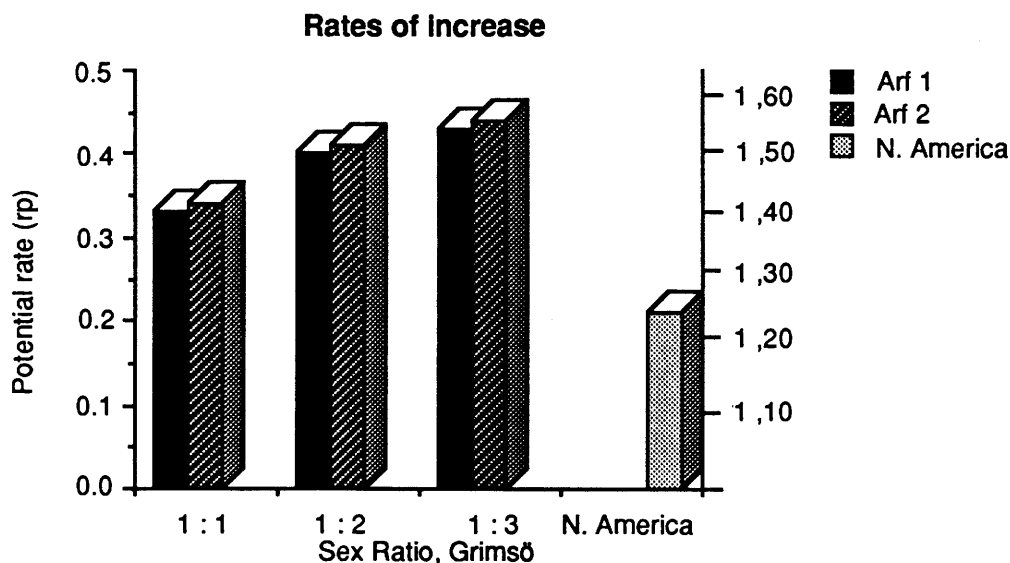


Fig. 2. Potential (r_p) and finite (λ) rate of increase in the Grimsö moose population at different age distributions and sex ratios calculated from the population in spring 1988. A comparison is made with average data from North American moose populations with little or no predation (Keith 1983, Van Ballenberghe 1983).

kg/km². Using the current market price in 1990 (\$ 12.8 US/kg), each km² in the Grimsö area will provide meat corresponding to \$ 956 US/year. In 1990 the total moose harvest in Sweden approximated 140,000 individuals, which equate to a market value of \$206 million US.

DISCUSSION

Abundant food (a large proportion of forest areas in young successional stages) and winters of moderate severity have allowed moose at Grimsö to be highly productive as indicated by natality rates. Although there is high browsing pressure in the area (Lavsund pers. comm.), forage was apparently still abundant enough to support a highly fecund female moose population. In contrast, the low productivity (few twin calves and few fertile yearlings) of female moose in some areas in Newfoundland was explained by overbrowsing, severe winters and low diversity among forage species (Bergerud *et al.* 1968, Albright and Keith 1987). Several moose populations in southern Sweden may poten-

tially be more productive in terms of calf recruitment (calves in autumn/winter in relation to adult population) than Grimsö, occasionally exceeding 60% annual increase (Stålfelt 1977). In contrast, populations in northern Sweden may barely reach 30% increase due to low fecundity and/or predation in combination with weather severity.

Adult survival is the most important variable governing the rate of increase in elk (*Cervus canadensis*), given that fecundity is stable (Nelson and Peek 1982). This is probably also true for Swedish moose. In order to achieve maximum rate of increase, adult survival rates for elk and feral horses must be ≥ 0.95 (Nelson and Peek 1982, Eberhardt *et al.* 1982). Low non-hunting mortality among moose at Grimsö appear to allow survival rates of the same magnitude over a number of years. Survival rate estimates in moose populations with no or few predators were similar to data from the present study, and hence adult survival may be $>80\%$, particularly among females (Mytton and Keith 1981, Gasaway *et al.* 1983, Albright and Keith 1987,

Fryxell 1987). Interestingly, most of the non-hunting deaths at Grimsö were caused by car accidents. "Natural mortality" may be kept at a low level because of absence of predators in conjunction with extremely high hunting pressure. The risk of being shot before 5 years of age was >90% among males and 70% among females. Therefore, few moose would likely be old enough to die of senility. The major difficulty in analysis of population dynamics of any wild animal undoubtedly lies in obtaining useful estimates of survivorships, especially among adults (Eberhardt 1985). Even if hunting mortality accounts for the major part of the deaths within the moose population, other mortality must be calculated and incorporated into population models to evaluate and/or suggest possible management actions. Such data are needed especially from northern Swedish moose populations where predation and weather may have a relatively larger impact on population dynamics.

Dispersal may potentially have a profound effect on the rate of increase in a population although few studies have tried to evaluate it. In one of the most dense moose populations reported from North America, finite rate of increase (λ) was still low (1.03-1.12) due to annual dispersal (Rolley and Keith 1980). The philopatric patterns among moose at Grimsö (Cederlund and Okarma 1988, G. N. Cederlund and H. K. G. Sand unpubl. data) indicated that emigration and immigration were of minor importance to demography of the study population. Philopatry may be due to one or a combination of factors: evenly distributed resources in a highly fragmented landscape, numbers of potential dispersers (subadults) are kept low due to regulated hunting, and the population is still below forage carrying capacity (no density dependent effects) (cf. Saether 1987).

The moose population at Grimsö had a much higher potential rate of increase than moose populations in North America. Keith

(1983) and Van Ballenberghe (1983) reported that the finite rate of increase (λ) in moose populations with adequate food, few or no large predators and light hunting pressure, ranged between 1.15 - 1.30. Variations in the rates of increase may be due in part to problems in obtaining accurate census data and unbiased data on survival and fecundity (Van Ballenberghe 1983). The calculated potential rate for the Grimsö population was probably less crude because relatively high quality data has been obtained on important variables such as age structure, age specific fecundity and density estimates.

Is the high potential rate of increase calculated for the Grimsö population equal to the intrinsic rate or maximum rate of increase (r_m) (Caughley 1977a) for moose? Small density dependent changes in fecundity as well as condition may have occurred in late 1970's and early 1980's compared to the years of this study (G. N. Cederlund and H. K. G. Sand unpubl. data). However, given a stable age distribution and sex ratio, we suggest that r_p may be unaffected up to densities up to between 2.0-2.5 moose/km². Crete (1987), also suggested that carrying capacity (K) for North American moose could probably exceed 2.0 moose/km² in a predator-free environment. The literature contains few estimates on density dependent processes in moose populations, either without or with low predation pressure (and hence neither r_m estimates) although it exists (Crete 1987, Gasaway *et al.* 1990, Boer in press). Density dependent effects on survival and fecundity have recently been shown for other cervids such as red deer (Clutton-Brock *et al.* 1982), elk (Sauer and Boyce 1983, Gogan and Barrett 1987), and for a variety of other large mammals (Fowler 1981a). Data from Finland suggested a relationship between reproductive traits and density, indicated by maximum calf production at densities around 0.4 moose/km² (Nygrén 1985). In some areas in Sweden statistics from annual hunts indicated a decrease in mean carcass weights

during the years of peak densities (Lönroth 1982).

There are no obvious signs that the Grimsö moose population is or has been above vegetation carrying capacity in spite of the relatively high densities. Consequently, we assume there is a linear relationship between population density and yield above the current density (approx 1.3 moose/km²). Big game populations are expected to be the most productive at levels resulting in some degree of impact on their resources (Fowler 1981a). Regional impact by moose on vegetation has been recognized on deciduous species and on pine plantations (Bergström and Hjeljord 1987, Lavsund 1987). Many local Swedish moose populations with crude estimates of calf recruitment of 30 to 60% of adult winter population (calculated from winter surveys and hunting statistics) may be close to a level producing maximum sustained yield (MSY).

Yield in a moose population can be influenced not only by age specific density dependence by skewing the yield curve (cf Fowler 1981b), but also by manipulating the age structure and sex ratio through selective harvesting. Seemingly small variations may have profound effects after a number of years (Van Ballenberghe 1983). Selection for bulls in the harvest have distorted sex ratios in many moose populations in Sweden and resulted in a preponderance of females (Markgren 1974). Together with selective killing of small and young females many moose populations may therefore, for a given density, not only contain an excess of females but also a proportionally high number of middle-aged females with high fecundity rates (cf. Markgren 1969, Saether and Haagenrud 1983). The potential rate of increase, and hence the sustained yield under such circumstances may be even higher than 60% annual increase ($r_p > 0.47$)

It is interesting to note that our calculated yield in terms of number of moose in the kill is equal to the harvest quota proposed by the

hunting authorities (90 moose in 1988). Maybe, despite Caughley's warnings (1977b), it is possible to make good predictions about next autumn's harvest from the proportion of calves in the population, obtained through hunters' observations and aerial surveys at Grimsö. We assume that density and age distribution are stable over time, survey methods accurate, and stochastic variations in death rate and fecundity are low. Calculations of long term data on annual surveys and harvests (H. K. G. Sand and G. N. Cederlund unpubl. data) indicate some instability in age distribution. This is mainly due to changes in annual harvest strategies that may have "residual effects" on age distribution, which are not observed in a cohort analysis. However, relative to many North American moose populations that may be more or less stochastically affected by a combination of factors like predation, hunting, weather and forage, the population at Grimsö has a potential rate of increase ($r_p = 0.40$) with small variations between years that are mainly caused by variations in hunting strategies.

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